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SOME DISEASES OF CEREALS CAUSED BY SCLEROSPORA GRAMINICOLA

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E. J. BUTLER, M.B., F.L.S

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AGRICULTURAL RESEARCH INSTITUTE, PUSA

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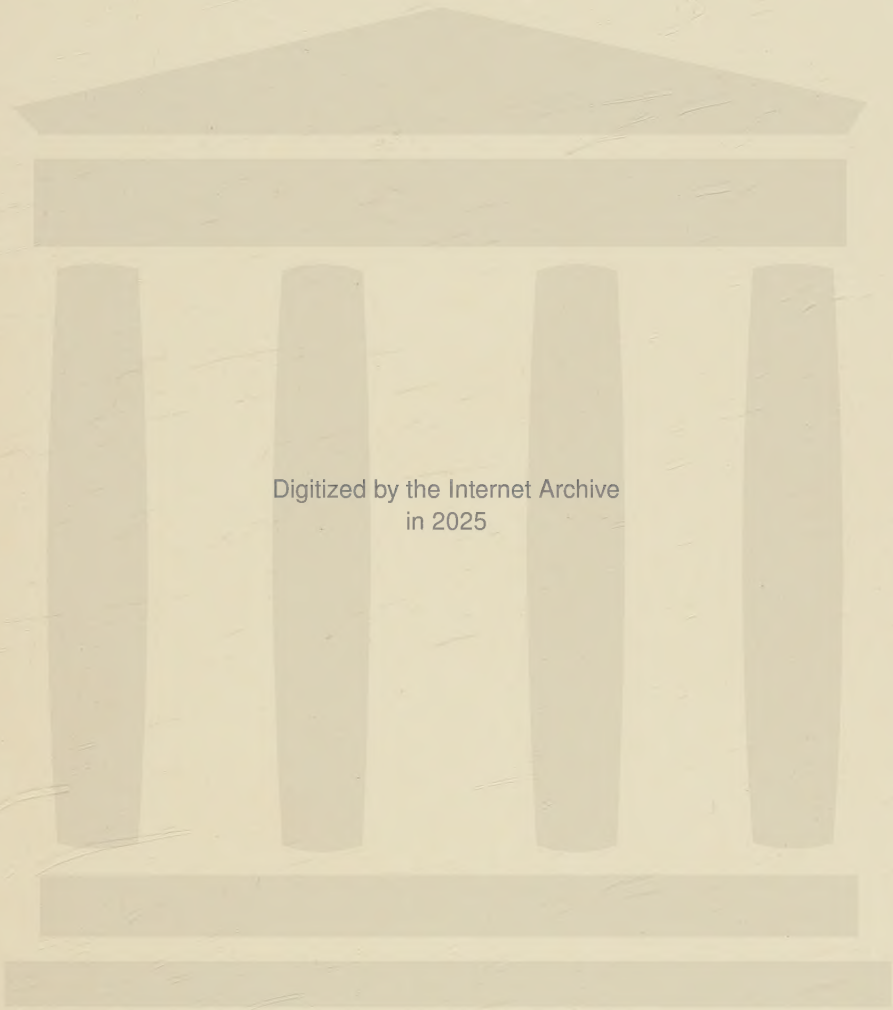

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PLATE I.

Ears of Pennisetum typhoideum affected by Sclerospora graminicola.

SOME DISEASES OF CEREALS CAUSED BY SCLEROSPORA GRAMINICOLA.

BY

E. J. BUTLER,

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A CURIOUS disease of Pennisetum typhoideum (*bajra*) occurs sporadically in most provinces of India where this cereal is grown. It is not usually of sufficient intensity to attract much notice; but at times, particularly in low-lying ill-drained land, it develops into epidemics of varying severity. Its chief interest is, however, at present pathological, for it is one of a small number of diseases, caused by parasites, which produce deep alterations in the reproductive parts of plants, resulting in great modification in the floral organs and entire or partial sterility.

The general appearance of diseased ears is represented in plate I. The spicate inflorescence, from which this species obtains its name of the bulrush millet, is transformed wholly or in part into a loose green head, composed for the most part of small twisted leaves. Every stage can be found between ears in which the greater part ripens its grain normally, only a small proportion showing the characteristic deformity, and ears entirely affected and absolutely sterile.

To understand the changes in the inflorescence to which this appearance is due, it is necessary, in the first place, to have a clear idea of the structure of the normal inflorescence. The *bajra* ear is composed of crowded spikelets arranged around a woolly, unbranched axis, the whole ear being up to a foot long, by one, or one

and a half inches broad. The spikelets (plate II, fig. 1) are pedicellate, the pedicel being jointed below a bristly involucre, which encloses usually one, but sometimes two to six (Prain) or eight (Gammie) spikelets. I have rarely found more than two on the diseased ears which are those that I have chiefly dissected. The rachilla of the spikelet is simple, and not prolonged beyond the upper floret. In the other Penniseti, when ripe, the pedicel breaks below the involucre which is carried on the fallen spikelet. In cultivated *bajra* the involucre is, however, usually persistent. The involucre consists of simple, or more usually, feathery bristles, unequal in length, but normally projecting slightly beyond the glumes. The lower two glumes on each spikelet are sterile ; the lowest being always minute and sometimes altogether absent. Its veins are not visible. The second is often also minute, but may be nearly equal to the fertile glumes, and is three, five, or seven veined. Both these are obtuse, or the first is occasionally, and the second more often truncate or retuse and ciliated near the tip on the margins. The third and fourth glumes are usually fertile ; the third enclosing a palea within which are three stamens. The paleæ and stamens are sometimes absent. The lower floret is, therefore, male or sterile. The fourth glume is paleate, and encloses three stamens and an ovary, or only the latter. There are two minute lodicules. The fertile glumes III and IV are boat-shaped, with a more or less shortly mucronate apex, ciliate at the margins, and with five or seven veins. The paleæ are enclosed by the fertile glumes, and resemble them except in being more delicate. On ripening, the fertile glumes and paleæ become hardened. Within them, in perfect florets, are two minute lodicules, three stamens with capillary filaments and versatile anthers, slightly bearded at the tip, and the ovary with a simple style crowned by two long stigmatic plumes.

The modifications undergone by diseased ears affect the secondary axes of the inflorescence only ; and certain parts of these to a much greater extent than others. The following account is based on the dissection of some hundreds of spikelets from about forty diseased ears. Owing to the variation which I have found

between individual ears, it is more than probable that changes other than those described will be found on further search.

1. The bristles of the involucre are very often hypertrophied, the hypertrophy affecting some only of the bristles (plate II, fig. 4). These are enlarged into tough, simple spines, usually non-plumose, ribbed, and showing various degrees of longitudinal torsion. They may be one inch long, by one-sixteenth of an inch thick, and may be flattened, round or angular. The upper part is sometimes spirally twisted, corkscrew-like. The bristles are also transformed in some cases into leathery, brown, flattened or contorted bodies, but they never show any approach to a leafy structure.

2. The pedicel sometimes bears two spikelets, the lower being laterally seated and sessile, a little way above the involucre (plate II, fig. 3). Only two spikelets have been seen thus, arising from the one rachilla.

3. The number of florets on a spikelet is sometimes increased to three or four (plate II, fig. 3, upper spikelet). One or two of these may remain as mere aborted buds, usually at the lower part of the rachilla.

4. In the individual spikelets the lower glumes I and II are never altered. As in normal ears they are often minute, and the lower usually difficult to see, and sometimes suppressed. The succeeding glumes III and IV, with their enclosed paleæ, are sometimes unaltered. More usually they are elongated, sometimes to over an inch in length (plate II, figs. 2, 3, 5). They never lose their character as glumes, and no division into sheath and blade was observed in any case, though they are occasionally virescent and usually softer and more membranous, than normally. Torsion, particularly of the upper part, often occurs ; and sometimes the glume is split into segments as a result of a local action of the parasite, which will be more fully described under the leaf alterations to be mentioned below.

5. The lodicules are unaltered or suppressed.

6. The stamens are variously modified (plate II, fig. 6) or suppressed. The changes affect both the filament and anther.

The former may be prolonged to a length of over half an inch, or reduced, so that the anther is almost sessile. It may remain capillary, or become flattened and plumose, particularly at the base (e, g). The anther may remain unaltered on the modified filament, or may be reduced (e), elongated (c), plumose (d), or, rarely, contorted. The whole stamen may be changed into a leafy structure, colourless or brownish, narrow, with nearly straight sides, usually ciliate and sometimes with a transverse fringe, marking a division into a sheath-like and a blade-like portion (k, l, m, n). When thus flattened, the middle is often marked by a distinct vein (l). Sometimes the stamen appears as a brown, leathery, pointed body, with no differentiation into filament and anther, and almost circular in transverse section, thus becoming staminode-like. No increase in the number of stamens was observed.

7. The main alteration takes place above the stamens. The central portion of the floret is usually prolonged in diseased ears into a leafy shoot, consisting of reduced foliage leaves, much twisted or malformed (plate II, figs. 2, 3, plate III, fig. 2). This proliferation occurs chiefly in the upper, perfect floret of the spikelet, but is accompanied usually by a similar, though less marked proliferation of the lower, male or sterile floret. Sometimes the two are nearly equally affected. The maximum length observed in leaves thus axially produced within the stamens, was three inches, and the maximum breadth one quarter of an inch. Usually a well-marked division into sheath and blade occurs, the sheath being often more developed than the blade, which may be very imperfectly formed and much inrolled. The colour is either green or brown. A tendency to longitudinal shredding is often shown, a feature shared, as will be seen below, by the diseased normal leaves of affected plants. Longitudinal torsion occurs here also, and usually there is some degree of crinkling into longitudinal or transverse folds, particularly in the blade (plate II, fig. 2).

In place of a simple axial leafy shoot, the centre of the floret may be occupied by a branched reduced shoot with simple, soft, brown elements, crowded together in minute buds (plate III, fig. 1). This condition appears to be rare. An intermediate stage

occurs sometimes in the prolificated male florets, where the centre may consist of four or five small, brown, simple or branched elements enclosed by the paleæ. Some of these may be staminodes, but the central ones are more probably reduced shoots, as it is difficult otherwise to explain the branching.

Central prolification of the floral axis in plants may be of different kinds. It may be what is often described as viviparity. This term appears to be very loosely applied in teratology. Strictly speaking, it implies the germination of the seed while still attached to the parent plant. It is also employed to denote sprouting of the inflorescence buds under similar conditions. But it is used, especially in the case of grasses, to cover cases of virescence of the outer floral whorls, or of prolification of the floral axis below the gynæcium, conditions in which it is difficult to justify the terminology. Thus Penzig (1894, Vol. II, p. 465) uses it to specify two cases described by Toumey (1891) of malformation in *Phleum pratense*, in one of which the floral glume was prolonged into a leaf, and in the other the axis above the glumes was elongated, and bore at its apex a perfect flower. It appears probable that many cases of so called viviparity in grasses, belong really to the class of changes next referred to.

This is the form of central prolongation of the axis of the flower called by Moquin-Tandon "median prolification" ("diaphysis," Englemann). Two varieties of this are described by Masters (1862, p. 360). In one, the new growth proceeds from between the carpels, which are formed, though they may be much modified. In the other the carpels are absent. The new growth is usually a flower bud ("median floral prolification," "floriparous diaphysis"), but it may be a leaf bud ("median frondal prolification"; "frondiparous diaphysis"). Masters points out that the change occurs very frequently in such plants as normally show a tendency to prolongation of the floral axis, indicated, for instance, by their having, free central placentation, or an enlarged thalamus (Rosaceæ, Ranunculaceæ), or elongation of the axis between two of the floral whorls, as in Dictamnus. The prolification is therefore in Masters' opinion one, not of the pistil, but of the upper segment of the floral

axis, which may occur either above the carpels or may involve them. Two instructive cases are described by Masters in this paper. In one, a species of Campanula, the calyx was free, the corolla double, the stamens with petaloid filaments, and in the place of the pistil, there was a bud consisting of several series of green bracts, arranged in threes and enclosing quite in the centre three carpellary leaves detached from one another and the other parts of the flower and open along their margins where the ovules were placed. In the other, a Fuchsia, the calyx was similarly detached from the ovary simultaneously with the extension of the axis. Here the petals were increased in number and variously modified, the stamens also ; while in the centre and at the top of the flower, conjoined at the base with some imperfect stamens, was a carpel open along its ovuliferous margin. These cases indicate a lengthening of the floral axis, immediately below the gynæcium, and in the second case the stamens were carried up on the prolongation.

The axial sprouting in the florets of Pennisetum in this disease, is a case of median frondal prolification, and belongs to the second variety of this, mentioned above, *i.e.*, that in which the whole segment of the floral axis, which bears the pistil, is prolonged, the pistil being at the same time entirely suppressed. In no case examined, was any trace of the pistil to be found. Further two cases were seen in which the stamens were carried up on the prolificated axis ; in one, three stamens arose from the dorsum of the outer leaf of the new bud (plate II, fig. 7*a*) ; in the other, two of the stamens occupied their ordinary position at the base of the bud, while the third was carried up, and arose a couple of millimeters above the other, on the outer side of the sheath tube of the first leaf of the bud (fig. 7*b*).

In one head examined, the greater part of the florets were produced into an axial horn, a hollow organ entirely closed at the margin and produced from within the staminal whorl. This was, in many spikelets, produced equally from the lower (normally male) as from the upper (perfect) floret of the spikelet. Though, at first sight, it resembled a hypertrophied pistil, its structure was

that of a leaf, and it must be considered as merely a modification of the commoner form of median prolification, in which the bud consisted, instead of a leafy shoot, of a leaf united at the margins to form a tube, within which, at the base, the rudiments of a second leaf were often formed. Hairs and stomata occurred on both surfaces, within and outside the tube wall. In some cases the union of the margins was imperfect, only occurring at the base, while the top was an inrolled blade.

It must not be supposed that all these changes occur in each diseased ear. As a matter of fact, there is the greatest possible variation between one diseased ear and another. In some, the bristles alone are affected, in others, the glumes show the most marked alterations, while in others median prolification is almost universal in the florets.

Besides the ears, the leaves of plants affected with this disease show more or less considerable changes. In young plants, or in early stages, many leaves may be seen with the usual fresh green colour changed wholly, or in part to whitish, and later to brown. The whitening of young leaves is visible usually as long streaks, often occupying half or more of the leaf surface, in transverse diameter, and extending almost the whole length of the leaf. In older plants the leaves affected are chiefly those from whose axils the ear stalks spring. These are more completely whitened than in younger plants, and the colour rapidly changes to yellowish brown. At the same time the leaf is deformed, being twisted and transversely folded, and shows a great tendency to shredding of the blade towards the tip (plate IV, fig. 1). This shredding is also shown in plate IV, figs. 2, 3, in other plants affected with the same disease, but is not usually so evident in Pennisetum, as in these. In old plants, when the green ears are fully developed, the upper leaves are mostly browned, and many of them similarly split. Many leaf buds in branching stalks are contorted, a mass of small white or brown twisted leaves being enclosed within the contorted outer leaf sheath (plate IV, fig. 1).

A considerable number of cases of virescence, prolification, and other modifications of the flowers of plants is known to be the

result of insect or fungus attack. Many instances of the latter are mentioned by Tubeuf and Smith (1897, p. 26) and Rostrup (1886). Thus Peronospora violacea causes the stamens of Knautia arvensis to become petaloid. Ustilago violacea causes the rudimentary stamens of the pistillate flowers of Lychnis dioica to develop fully. The reverse occurs under the influence of several Ustilagineæ, ovaries developing in staminate flowers, as in Carex præcox infected with Ustilago Caricis. Physoderma deformans Rostr. causes virescence and malformation of the flowers of Anemone nemorosa. The extraordinary hypertrophies and distortions of the flowers of Cruciferæ attacked by Cystopus candidus are well known. Molliard (1901) has even shown that parasites acting at a distance can produce these modifications; as, for instance, in Primula officinalis, where double flowers result from the attacks of a Dematium on the roots; and petalody of the stamens of Scabiosa Columbaria was experimentally induced by him by inoculation of the roots with Heterodera radicicola.

In grasses, several instances of floral modifications of this nature are known, the most important of which are caused by fungus parasites of the genus Sclerospora, one of the Peronosporaceæ. It is to one of these that the disease just described is due.

The mycelium of the parasite is found in all parts of the attacked plants which show the alterations mentioned above. Thus it has been found in the stem, leaves, rachilla, bristles of the involucre, glumes and prolificated shoots.

The hyphæ are large, unseptate, very variable in size, up to nearly 10μ in diameter, and run chiefly intercellularly (plate IV, fig. 4). They are found in the ground tissues of the stem, and the mesophyll of the leaves chiefly, but branches penetrate the bundle sheaths in the leaves, where they lie between the sheath cells, and others collect under the stomata and in young leaves send out clusters of condiophores through these into the air. Only in rare cases, chiefly in late stages, have hyphæ been observed in the inner walls of the epidermal cells sending haustoria into them. The xylem and phloem elements proper never contain the fungus,

though in some of the distorted bundles, where it is difficult to distinguish between the sheath and the outer layers of the xylem, cells may occasionally be found, apparently lying in the xylem, containing hyphæ. These are really sheath cells, infolded into the xylem by the distortion of the whole.

As in the case of several other fungi whose habitat is chiefly between the cell walls, some branches penetrate the latter and pass into or across the cell cavity. These intercellular hyphæ are of two kinds. The one are similar to the haustoria of other Peronosporaceæ, being simple or branched, thin-walled processes, arising from intercellular hyphæ, and sometimes forming small fungal clumps within the cells (plate V, fig. 1). The others correspond to the "Verbreitungshyphæ" described by Guttenberg (1905) in Ustilago Maydis, and like them are thick-walled filaments, often clothed with a distinctly two-layered cellulose sheath (plate V, fig. 3). This sheath, as in the maize parasite, consists of an outer portion deposited by the host cells around the penetrating hypha, in a defensive attempt to check its growth. The attempt often succeeds and the resulting thick-walled pegs projecting into the lumina are not uncommon (plate V, fig. 4). The inner part of the sheath is the wall of the fungus filament itself.

The intercellular mycelium is sparse in the stem and attains its greatest development in the leaves. The hyphæ frequently occupy the intercellular spaces at the angles of the mesophyll cells, but are also found in the lamellæ between two cells. They branch freely, have thick, rather gelatinous, cell walls, and clear protoplasm. In the stem, haustoria are not common, and are chiefly small, often button-shaped, processes, not unlike those of Cystopus. Their full development occurs in the leaves (plate V, fig. 1). Here, they are often extraordinarily numerous and usually simple or branched finger-shaped processes, sometimes much convoluted and occupying a fair proportion of the cell cavity. Their wall is thin while young, but older ones often have distinct cellulose caps (fig. 2) which are possibly provided by the host plant after the organ has ceased to be active, as in the case of Cystopus candidus (Guttenberg, 1905, pp. 8 and 9).

In fully infected leaves the mycelium is collected chiefly between the cells of the mesophyll adjoining the bundles and also in the inner layers between these (plate III, fig. 3). When sporangium formation is about to begin, tufts of mycelium reach the air chambers of the stomata, which are, as in many grasses, arranged in parallel, longitudinal rows, one on each side of each vein. Sporangium formation is accompanied by great assimilative activity of the fungus, which so increases its demands on the living cells of the host, as to cause the latter to collapse and finally die. Prior to this, the chlorophyll of the assimilating cells is wholly or in part destroyed, and starch is noticeably absent in the cells which harbour the haustoria of the parasite. Hence the pale streaks, which are the first indication that young leaves are affected, are visible before any conidiophores are extruded, and these streaks only turn brown, from death of the cells, after sporangium formation has reached its maximum.

The effects of the fungus on the tissues are evident both in the mesophyll and the bundles of the leaf. The former undergoes hypertrophy (''hyperplasie,'' Küster, 1903), the number of layers being increased without any modification in the structure of the cells. These remain always large, thin-walled cells, with small air spaces in the angles between adjacent cells. In the sheath, where a hypoderm of a single layer is often demarcated from the mesophyll on the upper surface, this may be increased to two or three layers. In the blade there is no hypoderm, and the increase takes place in the ordinary mesophyll layers, but is never considerable and is sometimes absent. On the whole, it may be said that the fungus occurs in greatest quantity in the blade of the ordinary leaves, and in the sheath of those produced by median prolification, and the hypertrophy produced is most evident in these parts.

In the bundles, the number and size of both the xylem and phloem elements are increased. In normal bundles of moderate size, the xylem consists of a central spiral vessel, with a second (annular) vessel, or an air space, inside it, and two large lateral vessels, one on each side. The phloem consists of a group of

sieve tubes with their companion cells. In diseased leaves, the vessels are increased in size and number, groups of two or three large vessels occurring on either side (plate IV, fig. 4). The sieve tubes are increased in number and are slightly larger than normal. These modifications occur both in the sheath and blade of attacked leaves. From the collapse of the central layers of parenchyma which follows on sporangium-formation, and the consequent flattening of the leaf, the bundles are, in old cases, often distorted, being broadened transversely or sometimes infolded, so that the xylem projects laterally outside the phloem. In these cases the large vessels are flattened to a remarkable degree (plate IV, fig. 5).

Sporangia are produced only on the normal leaves of the host, never in the inflorescence. Following on the appearance of the whitish streaks which are the first outward sign of the presence of the parasite in the leaves, a cloud of thick, pale conidiophores bursts from the stomata, covering the surface of the streaks with a greyish white haze easily visible to the naked eye. A single or several conidiophores may project from each stoma (plate V, figs. 5, 6). They are broad, rather short, stalks, measuring about 100μ in length, by 12-15μ, unbranched in the lower part, but usually with a few short, thick branches, dichotomously or trichotomously formed at the top, and crowned with numerous papillæ of characteristic shape, on which the sporangia are borne. The latter are hyaline, broadly elliptical, slightly pointed at the free end, with a thin smooth wall, and 22-30μ by 12-16μ in diameter. They fall early without any stalk, and germinate rapidly in water, liberating zoospores (plate V, fig. 8). The number of zoospores varies with the size of the sporangium, from three or four up to a dozen or more. They are irregularly kidney-shaped, unequal sided, flattened bodies, with two cilia from the concave side, the posterior of which is the longer (plate V, fig. 8). The zoospores after coming to rest round off, measuring 9 to 12μ in diameter in the quiescent state, and germinate rapidly by a hypha.

After the formation of sporangia the conidiophores early collapse, the whole asexual stage of reproduction being evanescent, and only to be found in young plants. Once the characteristic

deformity of the ears is visible, sporangia are not likely to be found.

Oogonia are formed in immense quantity, at a late stage in the life history of the parasite.* After fertilization they are large brown bodies, visible from their size and colour to the naked eye. They occupy the parenchyma of the leaf blades, both of the foliage leaves and of those formed in the inflorescence. Very rarely they occur in the sheaths of the foliage leaves and in the glumes, while in contrast to the foliage leaves, the sheaths of inflorescence leaves often contain them. They are often arranged in longitudinal rows on each side of the veins, as a result of oogonium formation taking place chiefly in the layers of parenchyma bounding the bundles, where, as already mentioned, the mycelium shows a tendency to collect. The ripe oogonium after fertilization, thickens its wall, which is closely applied to the wall of the oospore without, however, fusing. Hence, the whole fruit is characterised by the possession of a very thick wall in two layers, the outer of which is the oogonial wall, and the inner only belongs to the oospore.

The oospore is usually perfectly spherical, with a smooth wall, yellow in colour (Saccardo's "Chromotaxia" No. 23), and of even thickness all the way round. The oogonial wall, on the other hand, is deeper in colour, approaching tawny (between Nos. 31 and 32 of Saccardo), and is often irregular, being provided with thickenings, which gave the whole fruit an elliptical, angular or irregular shape, according to their position, but prevent it being ever quite spherical. The ripe fruit (plate V, fig. 9) measures 34 to 52μ in diameter (average of 25 measurements, 42μ), the oospore proper being 22·5 to 35μ in diameter (average of 50 measurements 32μ). After trials extending over two years, I have not succeeded in germinating the spores, though from the evanescent nature of the asexual stage, and the regular manner in which the disease appears in certain places every year, it is highly probable that this occurs

* A rough calculation, made by counting the number of oospores in a measured part of the field of the microscope, gave 480 oospores to the square millimeter, in a portion of leaf where they were arranged in an almost solid mass.

freely in nature under suitable conditions. My trials have been made in the north of the Gangetic plain where I have never observed the disease to occur.

Three other examples of Sclerospora disease of cultivated Gramineæ occur in India.

The first of these is common in some places on Andropogon Sorghum (*jowar*), and I have collected it from several parts of the Bombay and Madras Presidencies. It is also the disease referred to in Madras by Mr. C. A. Barber (1904, p. 278), under the heading of "shredding of the leaves." Any disease of this most important crop which holds the possibility of epidemic extension, as this certainly does, is worthy of note.

It occurs frequently on low-lying land and does not appear to be easily detected on young plants. The affected plants become whitened at the top, irregular streaks forming in the upper leaves. Axillary branches are frequently deformed, a crowded bud being held imprisoned in the sheath of the subtending leaf, or the internodes are shortened so that the leaves stand out in a fan-like manner. Later on the usual shredding occurs, from destruction of the parenchyma between the veins (plate IV, fig. 2). At this stage, or earlier, the oospores are distinctly visible to the naked eye as small reddish points, arranged in parallel rows. These have been found in the leaf blades only, not in the sheaths. The ears may or may not be affected. In many cases they are not formed at all. In others they are deformed and much reduced but without the profound alterations of the flowers seen in the ears of Pennisetum. Mr. Barber says that in attacked plants no grain is produced. Hence, complete sterility is possibly a feature of this disease, though I have not had sufficient opportunity to examine this question personally. No sporangium formation has been discovered.

Anatomically the fungus occupies the leaf blade chiefly, having the same general distribution in the tissues as in Pennisetum. A dense fungus layer surrounds the bundles in advanced cases, lying outside the bundle sheath. In this the oospores are chiefly developed. The hyphæ are not usually as large as in Pennisetum and are hence more difficult to see. Similarly the haustoria are

less developed, those seen being chiefly simple finger-like processes entering the parenchymatous cells.

Excepting for the absence of a sporangial stage, the fungus agrees with that on Pennisetum. The oogonia are similar in shape and colour and measure 38 to 50μ (average 41μ), thus being slightly smaller than on the first host. The oospores are 27 to 33μ (average 32μ), thus agreeing with the other. I can find no constant difference sufficient to refer the fungus on the two hosts to different species.

The third cereal disease caused by a Sclerospora in India is very briefly referred to by Mr. Barber in the same paper as the above. It occurs on Setaria italica in Madras, being very abundant in some parts. I have only examined specimens kindly provided by Mr. Barber, and have not seen it in the field. These showed the same distortion and shredding of the leaves as in the previous cases (plate IV, fig. 3). The latter were crowded with oospores, agreeing with those on the other hosts in shape and colour, and 36 to 46μ (average of twenty measurements 41·5μ) and 26 to 34μ (average of twenty measurements 30μ) respectively, in diameter. Hence, though the asexual stage was not observed, the fungus cannot be separated from those on the other hosts.

The last of the Indian Sclerospora diseases which I have seen was found on Euchlæna (Rheana) luxurians on the Poona Government Farm, in 1905. The sporangial stage alone was observed, and agreed perfectly with that on Pennisetum which was common in the vicinity. Only early stages of the disease were seen, and hence oospores could not be discovered. The host plant was being experimentally grown on the farm and is not, so far as I am aware, cultivated anywhere in India, though an important fodder in some parts of the world. The disease is therefore of minor importance in this country.

The whole of the characters of these fungi correspond to the type of the genus Sclerospora. Of this three species have been recognized in the most recent work on the genus, and a fourth should probably be added, to include Peronospora Maydis Raciborski (1897). Thus extended, it embraces all the Peronosporaceæ which

occur on grasses, and all of its members are found on these hosts, excepting the least studied, S. Magnusiana Sorokin, which was found by Sorokin on Equisetum in Russia.

Peronospora Maydis Racib. agrees entirely with Sclerospora in its asexual stage, differing from all other Peronosporaceæ in the broad, short conidiophores, with short, thick, dichotomously formed branches at the top, provided with broadly conical papillæ on which the conidia are formed. The mycelium and haustoria also agree, the latter being of the button-shaped type found in the stem of Pennisetum. The oogonia differ somewhat, having a not very thick, though persistent, membrane. This is not smooth, but provided with irregularly arranged, small, conical, warty thickenings. In the older descriptions the oogonial wall of Sclerospora was described as fusing with that of the oospore on ripening, but Berlese (1902, p. 69) is clearly not of this opinion, and it is easy to ascertain from sections or by long maceration that the two coats are perfectly distinct. In Raciborski's species therefore, the separation of the two walls mentioned by the author does not tell against the fungus being a Sclerospora. No doubt the figure accompanying the description is about as unlike the oospore of a Sclerospora as could be, but it is evidently highly diagramatic, and omitting the figure, the description would apply sufficiently to Sclerospora. In Berlese's Monograph it is also suggested that the species is a Sclerospora, but a definite opinion is not given there, and cannot be given here, in the absence of an examination of original specimens. The fungus causes the most intense cereal disease produced by the Peronosporaceæ, epidemic outbreaks in Java (where it is known as "lijer"), destroying whole fields of maize. It has not so far been reported elsewhere.

The remaining grass parasites of the genus have been critically examined recently by Traverso (1902 (1)). As a result of a careful study he gives the following classification, reducing to two the three species which had been usually accepted:

Oospore 28-35μ. d.; hybernating spore with undulated contour, with wall of the oogonium very thick, rubiginous. *Scl. graminicola.*

Oospore 40-60μ. d.; hybernating spore with smooth contour, with oogonial wall not or little thicker than that of the oospore, pale yellow. *Scl. macrospora.*

As an asexual stage has only been found in Scl. graminicola, Traverso bases his classification on the sexual stage alone. It is in this stage only, that the majority of students of the genus have seen their species.

Sclerospora graminicola (Sacc.) Schroet. has been recorded up to the present only on species of Setaria, chiefly S. viridis, but also S. italica, S. glauca and S. verticillata, in Italy, France, Germany, Austria, Russia, the United States and Japan. The influence of the parasite is very similar to that above described, virescence of the ears and distortion and shredding of the leaves being common. An excellent illustration of the disease of S. italica ("Awa") in Japan is given in Arata Ideta's Lehrbuch der Pflanzenkrankheiten in Japan (1903) with a description in Japanese. In this, the prolification of the spikelets and shredding and torsion of the leaves is well shown, and the fungus is clearly figured. It will be remembered that this is one of the cereals mentioned above, as being subject to Sclerospora disease in India. Similar effects on the other host plants have been referred to by several authors.

Sclerospora macrospora Sacc., under which Traverso, apparently with good reason, includes Scl. Kriegeriana Magn. (1895) occurs on a number of grasses, having been found in Australia on Alopecurus sp.; in Germany on Phalaris arundinacea; in France on oats; and in Italy in recent years, on wheat, maize, oats, Avena fatua, Agropyrum repens, Glyceria maritima (?), Phalaris coerulescens (?), Ph. arundinacea (?), Ph. canariensis, Lolium perenne, Agrostis alba (?), Holcus mollis (?) and Phragmitis communis. Its conidial stage has not been discovered. The Italian species, which was, after critical study, referred to this species by Traverso, was first considered by Peglion (1900 and 1901), who had chiefly investigated it in the field, to be Scl. graminicola. In the neighbourhood of Rome in 1899 a rather severe outbreak occurred in wheat, due chiefly, according to Peglion, to flooding of the fields by the Tiber in that year. The

ears were deformed and virescent, and no grain was matured in affected plants. The disease on this host has been several times observed since in different parts of Italy. A similar disease of maize was described by Cugini and Traverso (1902) near Modena, and its effects on this host as described by D'Ippolito and Traverso (1903) are similar to those of Scl. graminicola on Setaria. On the other cereal hosts mentioned above, the damage caused appears to be less considerable, and outside of Italy these new cereal diseases, which nevertheless are threatening enough, appear to have attracted little notice.

In the tropics I have been able to find only two references to disease produced by the genus, leaving out the "lijer" disease of maize. In neither is the parasite correctly determined. One is that by Mr. Barber (1904) mentioned above; the other a brief description of a Pennisetum disease, similar to that in India, from specimens collected by Dr. W. Busse in German East Africa, by F. C. von Faber (1905). In the first of these the parasite is taken to be probably one of the Chytridiaceæ, since the mycelium was not clearly seen, and the sporangial stage not observed. The resemblance of the oogonia to the resting sporangia of some Chyridiaceæ is considerable. In von Faber's paper the mycelium and oospores are described but not the sporangial stage, and the author was unable to determine if the Chytridiacean-like bodies (the oospores) were in organic connection with the mycelium, and attributes the disease to the mycelial infection. His description of the pathological changes in diseased plants differs somewhat from that given above. The glumes and bristles of the ear are said to be prolonged into leafy structures, a condition never seen in my specimens, and in the latter case difficult to accept on morphological grounds. The leaves are thickened by the development of a many layered hypoderm. Since, however, I have found a wide range of variation in the character of the deformity produced in different ears, it is quite possible that the action of the parasite in Africa differs from that in India. There appears to be no reason for supposing that the diseases are different.

It remains only to determine the species to which these Indian Sclerospora parasites belong. After a careful examination of all my material and comparison with the specimens of Scl. graminicola issued in Sydow's Phycomycetes and Protomycetes (Nos. 36, 37 and 165) and Scl. macrospora issued in Briosi and Cavara's Funghi parassiti No. 352, no doubt remains that the Pennisetum parasite is Scl. graminicola. This is somewhat surprising when we consider the much wider range of hosts in Scl. macrospora, while this is the first time that Scl. graminicola has been found on other hosts than Setaria. The sporangial stage agrees fully with that already described in Germany by Schröter (1879) and Fischer (1902), and in Japan as figured by Arata Ideta (1903), though the sporangia are larger, being 22-30μ by 12-16μ as against 20 by 15-18μ (Fischer). The sporangia are, however, variable bodies, since Berlese (1902) quotes measurements by Malbranche and Letendre, giving 12-15 by 10-11μ as the diameter. Scl. graminicola is so far the only species known to have this stage, if we omit Peronospora Maydis.

The hybernating spore also agrees. Traverso (1902 (1)) gives a very full description of the fruit and finds from a number of measurements that the oogonium averages 45·9μ in diameter and the oospore 32μ. The measurements given above for the Pennisetum parasite (42μ and 32μ respectively) agree in the most important item, the oospore, and are much smaller in both than the corresponding measurements for Scl. macrospora. The specimens in Sydow's exsiccata collected by Sydow on Setaria glauca near Berlin (No. 36) and by Kabat on S. viridis in Bohemia (No. 165) agree in measurements, and in the colour and shape of the fruit, very closely with the Indian fungus. Excepting, therefore, the difference of hosts the Setaria and Pennisetum Sclerosporas agree in all respects.

The fungus on Andropogon Sorghum corresponds with the above in the oogonial stage, which alone has been found. It is, of course, possible that sporangia will be found on this host also, when it is more fully examined, as I have not had sufficient opportunity for watching it on the living plant. In all the systematic

works which treat of Sclerospora the characters of the ripe fruit are taken as the basis for classification, and on this basis it is impossible to separate the species from Scl. graminicola.

On Setaria italica similarly, only oogonia and oospores have been observed in India. These are identical with the above in shape and colour, and are almost exactly the same size. As Scl. graminicola is already widely known on this host, this merely adds a new locality for its ravages. Traverso (1902 (2)) has found a special form. Scl. graminicola var. Setariæ italicæ—in Italy, differing from the type, in having larger oogonia and oospores ; but the fungus in India agrees in all respects with those on other Setariæ in Sydow's exsiccata and from the measurements given must be referred to the type species, not the variety.

Finally the fungus on Euchlæna luxurians agrees in its asexual stage with Scl. graminicola and, as no other species is known to possess this stage, may be referred provisionally to it.

Agricultural Research Institute,
Pusa, E. J. BUTLER.
12*th February*, 1907.

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DESCRIPTION OF THE PLATES.

Plate I.

General appearance of ears of Pennisetum typhoideum affected by Sclerospora graminicola (Sacc.) Schroet.

Plate II.

Effects of the fungus on the inflorescence of Pennisetum typhoideum.

Fig. 1. Normal spikelet of Pennisetum: 1. lower sterile glume; 2 upper sterile glume; 3 and 4 fertile glumes. P. paleæ. The upper floret is perfect, the lower male. X 7.

Fig. 2. Spikelets showing prolification. Figures and letters as before. X 1½.

Fig. 3. Pedicel with two spikelets arising above the involucre. That on the right and lateral bears two florets, f. 1. the lower, f. 2 the upper. That on the left and terminal bears three florets, f. 3., f. 4. and f. 5., 1. 1. lower sterile glumes; 2. 2. upper sterile glumes; 3. 3. 3. 3. 3. fertile glumes; P. P. P. P., paleæ; the floret, f. 3. being without a palea. s. s. s. s. s. the axial leafy shoots in the centre of each floret. These consist of a small number of narrow leaves, inrolled and contorted. X 1½.

Fig. 4. Hypertrophied bristles of the involucre. Natural size.

Fig. 5. Modified glumes from affected spikelets. Natural size.

Fig. 6. Modified stamens from affected spikelets. See text pp. 3 and 4 for further description. X 2.

Fig. 7. Stamens carried up on the prolificated shoot. Natural size.

Plate III.

Fig. 1. Apex of the floral axis of an affected spikelet, consisting of a cluster of bud-like structures on a branched stalk. X 16.

Fig. 2. Dissection of two spikelets borne on one pedicel, as in Plate II, Fig. 3. i involucre of unaltered bristles; 1. and 2. lower and upper sterile glumes; 3. fertile glumes; P. paleæ, there being

none on two of the florets ; st. stamens variously altered, and with two suppressed in the floret on the right ; s. prolificated shoots arising within and above the staminal whorl. In the left hand floret this was a simple horn. In the others it consisted of some contorted reduced leaves, which have been in part dissected out in the two right hand florets.

Fig. 3. Diagram showing the position occupied by the fungus mycelium in the mesophyll of the leaf of Pennisetum.

Plate IV.

Fig. 1. Contorted leaf bud of Pennisetum typhoideum affected with Sclerospora.

Fig. 2. Leaf shredding in Andropogon Sorghum affected with Sclerospora.

Fig. 3. Leaf shredding in Setaria italica affected with Sclerospora.

Fig. 4. Section of an infected leaf of Pennisetum showing the distribution of the fungus hyphæ in the mesophyll and adjoining the bundle sheath.

Fig. 5. A leaf bundle distorted as a result of the action of the parasite in causing collapse and flattening of the mesophyll cells.

Plate V.

Fig. 1. Haustoria of Sclerospora graminicola in the mesophyll cells of an infected leaf of Pennisetum. On the left simple and branched finger-shaped haustoria, the type which predominates in the leaf. On the right two club or button-shaped haustoria, a type more commonly seen in the stem. X 500.

Fig. 2. Old haustoria with a distinct cellulose cap. X 500.

Fig. 3. Intracellular hypha, showing the wall of two layers, the outer of which connects with the cell wall and belongs to the host plant. X 500.

Fig. 4. a. Intracellular hypha running obliquely across two cells. Note the very thick wall and almost occluded lumen ; b. b. peg like processes projecting into the cells, but arrested in further growth by the deposition of a thick cellulose cap. X 500.

Fig. 5. Conidiophores of Sclerospora graminicola from Pennisetum after the sporangia have fallen, showing the mode of branching. X 400.

Fig. 6. Conidiophores bearing immature sporangia. X 400.

Fig. 7. Conidiophore with mature sporangia. X 400.

Fig. 8. Sporangia germinating after having fallen into water; and zoospores. From Pennisetum. X 500.

Fig. 9. Oogonia and oospores of Sclerospora graminicola, after ripening: a. from Pennisetum typhoideum, b. from Andropogon Sorghum; c. from Setaria italica. Optical section, diagrammatic. X 550.

PLATE II.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

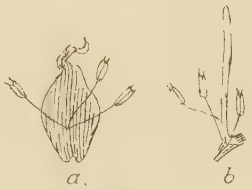


Fig. 7.

Fig. 6.

PLATE III.

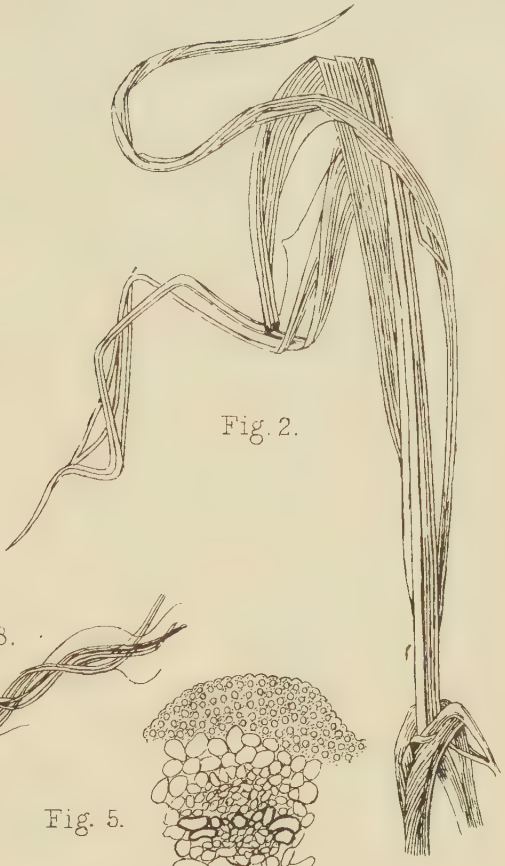
Fig. 1.

Fig. 2.

Fig. 3.

PLATE IV.

Fig. 1.



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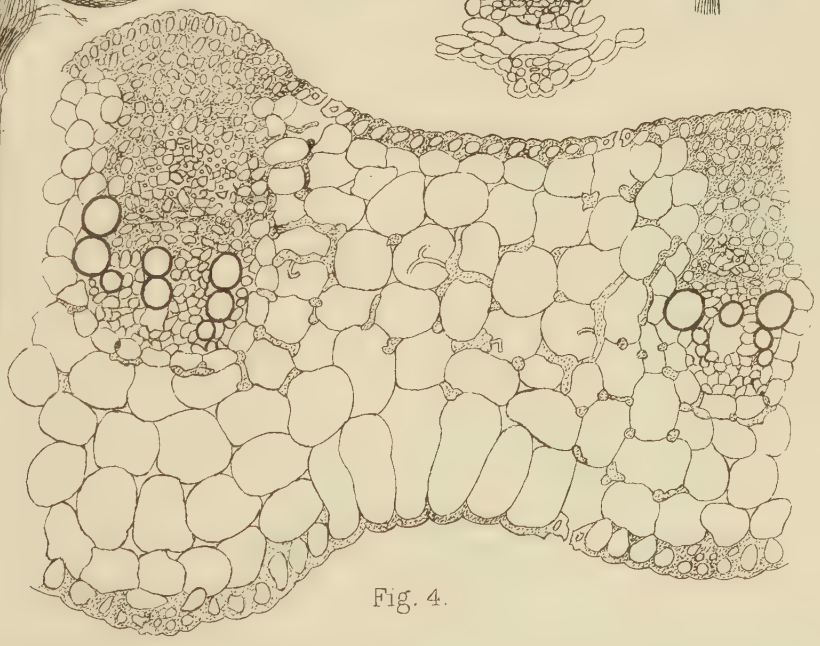
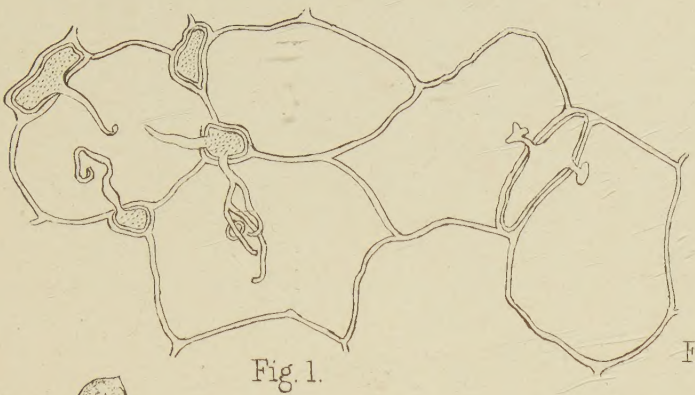


Fig. 4.

PLATE V.



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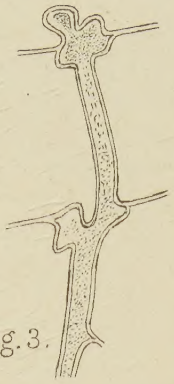

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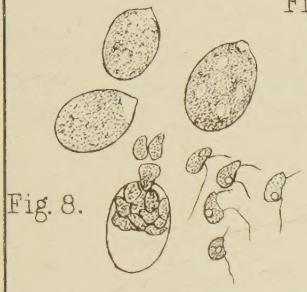

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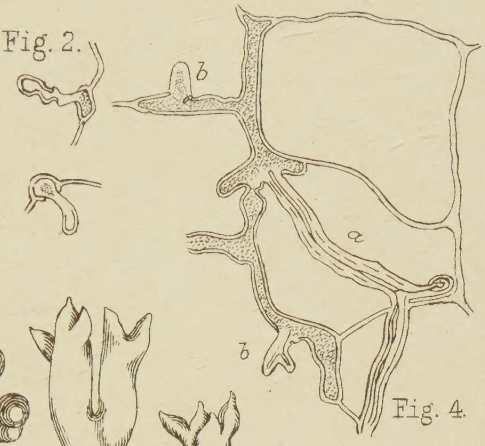

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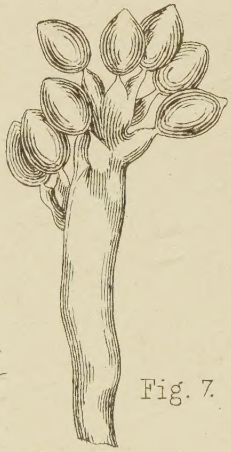

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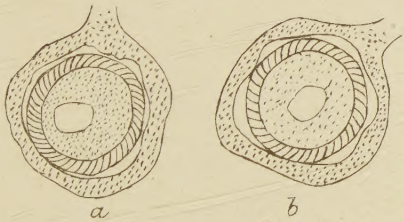

Fig. 9.

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